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BIRD-WATCHING AND BIOLOGICAL SCIENCE.

SOME OBSERVATIONS ON THE STUDY OF COURTSHIP IN BIRDS.

BY JULIAN S. HUXLEY, B.A.¹

THERE is to-day, most unhappily, too often a gap between the amateur naturalists and the pure field-workers on the one side, and the trained biologists on the other. The blame, as usual, cannot be laid to the account of either, for both are guilty. On the one hand the professionals fight shy of amateurish methods and failure to see principles behind facts, while the amateur dislikes (often with justice) the other's dogmatism and his reliance on purely laboratory methods.

It is the purpose of this paper to try and show how, in ornithology at least, this gap may be bridged. There is a vast army of bird-lovers and bird-watchers to-day in existence, whose enthusiasm needs only to be properly directed to lead them into most absorbing fields, and at the same time to provide all-important material for fundamental problems of biology.

Three things only are needed:—A knowledge of what to search for, a method to guide one's searching, and instruments to use in the search. The instruments lie ready to our hands. It was, I believe, Charles Dixon who was one of the first to realize that the prismatic binocular had so enormously enlarged the potentialities of field observation. The possession of one of these instruments, though not absolutely indispensable, is of the utmost importance. In selecting a glass three chief points are to be considered. The first is high magnification, which enables the observer to catch the details of attitude and expression which are so important. The second is high light-gathering power and definition, which depend on the size of the object-glasses. Without this, high magnification is a snare and a delusion, involving strain on the eyes. The third is quick adjustment of focus, for following the action of moving birds. Many glasses are made with independent focusing adjust-

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ments for the two eyes; these are useless for the bird-watcher. Some form of simultaneous adjustment is necessary, and in many ways the old pattern Goerz-Trieder longitudinally-moving focusing-head was preferable to the transversely-moving heads now in general use.

A magnification below six diameters is of little use; eight or ten is probably the best for general purposes, although even 12 will give satisfactory results. Besides a binocular, a telescope is often useful, especially for the larger and more wary birds. One with an object glass of at least two inches, and a magnification of about 25 diameters can be highly recommended. The price is comparatively small, and a little practice is all that is needed to handle it; one soon becomes so proficient that it is easy to follow even Swifts or Swallows in their aerial evolutions.

The efficiency of both the telescope and binocular can be considerably enhanced by a suitable stand. One that I devised for myself consisted of a camera-tripod with a kodak ball-and-socket joint attached; this in its turn screwed on to an apparatus composed of two pieces of wood lined with leather and joined by a long screw which holds the binocular in place. A special heavy ball-and-socket joint is also made by opticians for use with telescopes. By this means the fatigue and strain of holding the glass in place is done away with, and one's hands left free to take notes.¹

Before we go any further into the practical details of what to look for and how to look for it, it will be necessary to make what will perhaps appear a long digression on the theoretical side. The main biological problems demanding solution seem to me to be connected with the courtship of birds, and to that subject I shall here confine myself.

However, as I myself very soon discovered when I began working at the problem of Courtship, to get a real insight into it one must have a working knowledge of the theories of Evolution, the theories of Sex, and the theories of the Animal Mind. On these subjects I must refer the reader to the general works of Darwin, Weismann, Morgan and Washburn cited at the end of this paper. Here I will merely say that all my observations have gone to root

¹ See Huxley ('14), p. 529.

deeply in me the conviction that birds have a mind of the same general nature as ours, though of course more rudimentary: if they are automata, then so are we. Prof. Washburn's book reaches the same conclusion. As far as the problems of sex are concerned, bird-watching has led me to important ideas, and has gradually made me believe that in birds at any rate an individual of either sex contains within itself the characters of the other sex in a latent condition.¹ With which preface let us plunge *in medias res*.

It is an old idea, and a favorite of Sir Thomas Browne, that

¹ This is not the place to discuss the theoretical aspects of the problem of sex. However, it will be well to mention one or two ideas to which such studies as these have led me.

Morgan, in his recent book just cited, brings forward various facts, largely as the results of castration experiments, to show that the *mechanism of sex determination* is entirely different in birds and in mammals (and again in insects). This is an important and notable fact, but in considering its bearings we must not be led to forget another equally important fact that emerges especially as the result of a comparative observational study — namely, that all the determinants for the sexual characters of both sexes are present complete in each individual of either sex (with certain exceptions when the male has different sex-chromosomes from the female), that this holds good for both birds and mammals, and that the different results in the two groups are due to differences in the *method* by which in any individual the right characters are brought out, the unneeded ones inhibited. This is shown very well by the fact that the requisite mechanism for the copulatory actions of both sexes appears to be present in individuals of both sexes. For instance, I learn from my friend Mr. W. M. Winton that he has personally seen two cases of bitches where ovariectomy was followed by the acquisition of male actions. Similar actions in non-operated female animals are familiar in cows (Muller, *Sexualbiologie*), and are recorded for rabbits (Washburn, *in litt.*). Pearl and Surface have recently recorded (*Science*, April 23, 1915) a most interesting case where a cow assumed not only the behavior but also the appearance of a bull, owing to cystic disease of the ovaries. These examples alone will show that in mammals the female carries within herself the determinants for the characters of the opposite sex, just as Morgan's results show the converse of this to be true.

In birds, the facts assembled by Morgan show at once that the female carries the determinants for male characters. For the converse proof, I have myself assembled some records where the male performs female actions (and *vice versa*), in my paper on the Grebe (Huxley, '14). The case of the Phalarope is, from a different point of attack, proof positive that the determinants for female characters are present in the male. In all species of Phalaropes (Phalaropodidæ), while both sexes assume special plumage during the breeding season, and while this breeding-plumage is of the same general pattern in both sexes, and is obviously a recent acquisition in evolution, yet the female is larger and much brighter than the male, and in addition does all the courting. The only interpretation of these facts appears to me to be that, just as in most sexually dimorphic birds the male has acquired certain colors and structures, and that these have come to be shared by the female in lesser degree (Cardinal and many other Finches, Bob-white and most other Odontophoridæ, many Woodpeckers, Yellow-headed Blackbird, Dickcissel, Scissor-tailed Flycatcher, etc.), so here sexual selection has helped the female towards her bright plumage, and the male has automatically come in for his share. The results are best interpreted if we suppose (as is cytologically reasonable) that the determinants for the characters, even though the characters themselves are acquired primarily by one sex only, at once come to be present in the germ-plasm of both sexes. Suppose it to be the male which acquires the secondary sexual characters. After this there are two possibilities. Either the inhibition in the female will not be sufficient to restrain some appearance of the new characters in her, even from the start: or else in some unexplained way the inhibition will gradually weaken and the female come in the

man is a microcosm, exhibiting in miniature all the activities of a universe; and as far as marriage customs go, the idea is a true one. In the single species Man are found many varieties of marriage — promiscuity, polyandry, polygamy, and finally monogamy in all its phases of refinement — in origin largely a hateful economic necessity, yet in the outcome proving itself divinest of possibility. Almost every variation that is found as a mere fluctuating phase in the history of man exists separately, as a rigid law, for some species of bird. Bateson, in one of his lectures, gives us an imaginary conversation between a Pigeon and a Barndoor Fowl. The Pigeon rebukes the immorality of the Fowl's polygamous estate, while the Hen retorts that the Pigeons neglect the welfare of their race by confining themselves to a single mate. The Fowl and the Pheasant have Harems of the Orient, one cock owning more wives than another less successful bird. The Blackcock's system in some ways recalls that imaginary one of Plato's, for here there is no marriage, but the males have their appointed station, and their duties are over when the hens have come and chosen out the best. Still more mixture of promiscuity with polygamy is found in the Ruff. There are savage combats in the Thrushes, tournaments and jousts in Redshank and Blackcock. The chase is as frequent an adjunct of courtship as it was, if we are to believe the poets, with the Greek gods and nymphs, and as it is in many savage tribes to-day. And if one watches a pair of Red-winged Blackbirds or Mockingbirds in such a pursuit, he is inevitably driven to the conclusion that sometimes at least there is in it a thrill of pleasurable excitement for the female, of which she is fully conscious, even to the extent, I think, of sometimes provoking the chase.

When there is a monogamous union, it may be a temporary one, for the season only, as in most birds, or a true life-marriage, as in most Crows and Hawks.

Some birds lay down that "a woman's place is in the home," and the hen exclusively undertakes the duties of incubation. An extreme case of this deprivation of freedom of the female is seen

course of time to resemble the male more and more closely. Whether or not this second process actually takes place, we do know of course that the inhibition can vary in extent, as is shown by the Reindeer, where both sexes now share a primitively male character, or the Pheasant, where the female shows practically total inhibition of the male characters, for the purpose of protective coloration. The decision between these two possibilities must at present be left open.

in the Toucans, where the cock walls up the sitting hen in her nest-hole in an old tree; there she remains, fed by him, till the young are ready to fly. Other birds come more near to the ideal of the women's movement of to-day; in them both sexes share the duties of the pair more equally, and in all activities realize themselves equally and to the full. The Grebes, the Herons and the Swans will serve as examples. Sex-difference and sex-consciousness in these seem to be less, and as a result, just as in Man in similar case, there is in their courtship and the whole of their mutual relation, not so much emphasis on the less real, less great things that depend on sex-difference — coyness, timidity, helplessness in the female, eagerness, vain display, superior physical prowess in the male — and more emphasis on the things that are more fundamental, because belonging to the race instead of to one half of it alone — enjoyment of what is to be enjoyed, sharing of what is to be shared, joint action, mutual help. Let anyone study the relation of the sexes in such birds and compare it with the sex-relation in species with marked sexual dimorphism; then think of what is meant by the logical outcome of the chivalric, mediæval idea of woman's place, and compare that with the ideal behind the better part of the woman's movement of to-day, and I believe he will understand what I have in mind, difficult though it be to put into words.

Restricting ourselves to facts rather than interpretations, it will be found that the majority of passerine birds are monogamous, pairing for the season only, — temporary marriage. The duration of this tie is very variable; it may last until the nest is built, until the young are hatched, until the young are fledged, or it may be merged in a family life lasting through the winter.

Some of the monogamous species are dull-colored altogether; in others the cock is more brilliant and does most of the courting; while in still a third group *both* sexes are adorned with colors or structures that are employed in courtship.

Other birds have true marriage; they pair for life. Such are the majority of Falcons and Hawks — in whom, however, the problem is made interesting owing to the fact that the hen bird is larger, more powerful, and more active than the cock.¹

¹ See F. Heatherly, ('13), where a magnificent series of observations and photographs on a single pair of birds is recorded.

At the other end of the series we get such birds as the Ruff (*Machetes*) which is polygamous, but still shows a certain degree of promiscuity as well.¹

Other polygamous birds, such as the Peacock and the Pheasants, have more definite harems; while in the curious and beautiful little Phalaropes, the whole normal relation of the sexes is reversed, the hens in bright-colored plumage courting the cocks, who in their turn undertake all the duties of incubation.

Enough has been said to show the variety and interest of these relations alone. By collecting all available data we shall first of all be able to correlate the marriage-habits with the classification. Since the classification is by now fairly natural, or in other words, since it groups together those species of birds which are related by descent, we shall then be able to trace the evolution of the various customs and instincts — to see what was the most primitive condition, and to trace out whether polygamy and other specialized habits have arisen once only, or independently many times over.

This is important from the purely zoological point of view; it will also throw light on various problems of Evolution, notably on the question of Parallelism or the repeated origin of one adaptation from different ancestral stocks.

It is obviously of great interest to the Sociologist, since here he can trace the beginnings of all sex-relationships, in creatures where emotion is not yet complicated by reason. And if we study the details of each history carefully enough we shall, I hope to show, be able to interpret the phenomena of consciousness — the emotions and desires that lie behind the actions, — with sufficient accuracy to bring much grist to the mill of the comparative psychologist. Do not think me fantastic if I say that, even in birds, I believe that the finest emotions and most comfortable happiness are, as in man, associated with that form of monogamy in which male and female bear approximately equal parts. To support my opinions I will refer the reader to those of Selous ('13, pp. 298–299) elicited by his watching of Wild Swans.

Three years ago such words would have been almost without meaning to me; it was not until I had spent weeks watching the

¹ See Selous' exhaustive paper in the *Zoologist* for 1906.

behavior of a single species¹ and more weeks trying to think out the meaning of my observations, that there came to me the point of view — a combination of the evolutionary, the psychological, and the physiological — which made that statement possible. It was forced upon me by the facts I saw; and those who wish to penetrate into those arcana and mysteries of science where the beginnings of Consciousness are being shaped and added to Life cannot do better than observe the behavior of a single species of wild bird or mammal, and, having observed, try to understand.

But this is a digression. Let us return to our consideration of the question of courtship. First and foremost comes the need for facts. It is important for the professional biologist to have many new facts. To get these he must turn to the naturalist and the bird-watcher; and for these latter it is enormously important to have the old facts summarized and correlated into principles, for otherwise they will be unconsciously biased by preconceived notions. In such questions as these of sex-relations, we tend to have an unconsciously-held theory of our own, based upon every-day experience of our own species and of domestic animals; and not merely that, but since the questions are in Man associated with morality, we tend to see what we want to see, even in animals.

Our first duty as scientific observers is to try to get a clear idea of the usual sequence of events. The majority of birds are monogamous, and among them the majority again pair for the season, the two members of the pair separating during the autumn and winter, and pairing again, usually with new mates, before the next breeding season. Such species can then be considered typical, and we will begin by describing what may be called the "Annual Love-History" of such a species.

The pairing-up occurs remarkably early, often months before any eggs are laid. St. Valentine's Day is the traditional day for birds to pair; but in many species pairing-up may occur before this. Then follows a long period before consummation — a true engagement — in which the pair is constantly together and various displays by one or both of the sexes take place. Later, well on in the spring, comes the true marriage, when sexual consummation

¹ Huxley ('14).

takes place. At the same time nest-building starts, and very shortly the eggs begin to be laid; and then follow in turn the period of incubation and the period when the young are still unfledged and must be constantly fed. Then the nest is left, and a period of family association starts, during which the fledged young are being taught to find their own food and fend for themselves. This family life may break up very soon (*e. g.* in August; the English Robin) or may last right on through the winter until the next pairing-season (many *Paridæ*).

Most of this is common knowledge. Recent work, however, is extending our knowledge in two ways. First, it is becoming clear that in many species pairing-up is even earlier than was supposed, sometimes even in November or December, and also that in a good many species which were supposed to pair for the season only, the union is really for life, the pair preserving its identity through the winter, sometimes even when flocks are formed.¹

In the second place, we are beginning to understand the relation of the so-called "Courtship-actions" — the displays and dances and songs — to the annual history. For example; there is often no display at all previous to the period of pairing-up; then — most interesting point of all — there may be a long period when "Courtship" (in the sense of active display by one or both sexes) may be very much in evidence, although the birds have already paired-up into couples, but coition has not yet taken place.

However, I think that it will be as well to look at some concrete examples of the various sorts of sex-relationship found in birds. I will take three, all more or less non-typical, to illustrate the great variety that exists in this matter of courtship.

I make no apology for beginning with a life-history which I have myself investigated — that of the great Crested Grebe ² — for here I am sure of every fact.

In this aquatic species the two sexes are almost identical. Both are adorned with a beautiful crest, composed of two black ear-tufts and a ruff of chestnut, black, and pure white; this crest is very slightly less developed in the hen than in the cock, but is used exclusively in courtship, and used equally by both sexes.

¹ *e. g.* the Dabchick (*Podiceps fluvialis*), as reported by Mr. Mottram in a letter to me.

² Huxley ('14).

The birds generally go to the sea in winter, in small flocks or alone, returning to inland waters to breed in January or February. There, in February, pairing-up takes place — a process not yet wholly disentangled, but certainly associated with a great deal of flying and chasing (it probably resembles what happens in the Killdeer; *vide infra*). After this the pairs are very faithful — there is strict marriage for the season, preceded by a long engagement, for coition never takes place except on the nest, and nest-building does not begin till April. Quite soon after pairing-up, courtship activities begin, so that here, at least, pairing-up precedes any employment of the courtship structures (ruff and ear-tufts).

There are two entirely different sets of ceremonies gone through by the birds — ceremonies of mutual display, and ceremonies connected with coition.

The ceremonies of mutual display are extremely elaborate. There are three main divisions. The first is the simplest. Two birds that have been feeding or resting near each other will suddenly be seen to approach and to start shaking their heads at each other in a most peculiar manner, stiffly and formally, having first erected their crests and stretched their necks upwards to their fullest extent. After shaking for a certain time — a few seconds to a minute or two — they desist, and resume normal life.

The next form is amazing to see. It resembles the first in that it takes place as a mere interlude to the duties of every day, but is more elaborate. It starts with a bout of shaking which differs from the ordinary only in that it is prolonged to twice the usual length of time, and is followed by the remarkable diving for water-weed and the breast to breast collision which I have called the "Penguin-dance."¹

After this performance (which, I think, was the most thrilling sight I have ever seen while watching birds, with the possible exception of a Heron turning a succession of somersaults vertically downward from a height of several hundred feet to near the ground) they simply once more relapsed into ordinary existence.

The third form of display is mainly used when the two members of a pair have been separated. One will call for its missing mate. When the mate recognizes the call, it will swim in that direction,

¹ See Huxley, '14, pp. 499-500.

and finally dive. On this the calling bird changes its whole demeanor, spreading its wings out to display the white bar upon them, erecting its ruff, and drawing back its head, now rayed like the sun, on to its breast, white and puffed out. The diving bird approaches just below the surface, raising a ripple as it comes, and finally emerges just behind its mate in a strange stiff attitude: — “He seemed to grow out of the water. First his head, the beak pointing down along the neck in a stiff and peculiar manner; then the neck, quite straight and vertical; then the body, straight and vertical too; until finally the whole bird, save for a few inches, was standing erect in the water.” From this extraordinary position the bird will gradually settle down on the water; its mate meanwhile turns round, and the two finish with a bout of shaking.

The most noticeable thing about all these ceremonies is that they are “self-exhausting” — they do not lead on to anything further. Looked at from the psychological point of view, they seem to me to be nothing but “expressions of emotion”: the birds act thus because they are impelled to do so, because they enjoy it. Looked at, on the other hand, from the evolutionary point of view, they seemed to have been developed as a bond to keep the pair together.

In the other set of ceremonies, those connected with coition, the crest is not employed at all. The whole thing is more or less symbolic, the birds expressing readiness to pair by going into the extraordinary attitude adopted by the female during the actual act of pairing, when the bird “lies along the water” with neck outstretched to its fullest extent. The chief point to be remarked is that both cock and hen may adopt this attitude; indeed the proper qualities of either sex seem in this bird to have been in large degree carried over to the other.

There is one further interesting point to mention, namely, that *flirtation* is found in this species; by which I mean that one member of a pair (either cock or hen), if its mate is absent or unresponsive, will go off and perform the courtship ceremonies with a stranger. For further details, and for the jealousy thus produced, I must refer the reader to my original paper, merely remarking that we find some parallels to human affairs that give much food for thought.

In this species, then, we have elaborate Structures used only in

courtship, elaborate Courtship-actions gone through by both sexes, as a form of enjoyment (like a dance). We have Engagement and Seasonal Marriage, not exempt from Flirtation; we have special Coition Ceremonies, again shared equally by both sexes. We have in fact a Courtship which to one, like myself, who was familiar only with the facts adduced by Darwin and his followers, was a complete revelation — something entirely new and unexplained.

We will now turn to a modern investigation of a species which has figured prominently in the sexual selection doctrine from Darwin's time to the present. In the Blackcock (*Tetrao tetrix*, fam. *Tetraonidæ*) Selous¹ has made a series of careful observations, which show how totally different is the series of events in a species which exhibits marked sexual dimorphism combined with polygamy. The main unquestioned facts may be briefly stated. The cock birds are magnificent in a plumage of sheeny bluish-black with beautiful lyre-shaped tail. On the wing and tail are patches of pure white, while over the eye is a streak of scarlet. The female is so different as to merit a distinct name, the Greyhen; she is much smaller and of a dull reddish brown color speckled with black — a purely protective scheme of coloration. In these birds *the pair does not exist as a unit*. In April and May the cocks assemble early in the morning at regular meeting-places and go through various remarkable courtship-actions. The hens visit these assembly-grounds, and there coition takes place, several hens often mating with one cock. These are the main facts; their interpretation, as always, has depended on the closest watching of the details. Selous finds that what really happens is as follows. The cocks have definite stations or territories of their own on the assembly-ground, which they do not leave except under the influence of violent excitement, such as jealousy. Their actions fall into three main categories: — the ecstatic *dance*, not executed specially before the hen; a *display* performed directly to the hen and battles (which, however, are in reality but jousts, or sham-battles) between cocks.

The dance has often been described; at its most violent, it must be an amazing spectacle. The tail is spread out and erected, the wings a trifle drooped, the head alternately raised and lowered.

¹ Selous ('09).

In this attitude they run and leap over the ground, often turning partially round in the air, getting more and more violent as they go on, until, like Dancing Dervishes, they have made the dance an ecstasy of violent motion. Selous only once saw this dance in its perfection; but there are always rudimentary stages of it to be seen, when the birds, in the position described, would walk or run quickly over the ground, with now and then a little leap. The whole process, especially in these incipient stages, seems to be merely an outlet for the strong sexual emotion of the cocks, for they perform in this manner even when no hens are on the ground.

At intervals, hens visit the assembly-place; it is very rare for many to be there together. The arrival of one is usually signalled by a general commotion among the cocks, all leaping and dancing as above described. As, however, she walks from one part of the ground to another, each cock displays before her as long as she is within the limits of his particular territory. This display is entirely different from the dance. Instead of being a wild expression of passion, it is pompous and slow, and is adapted for showing off all the colors and contrasts of the cocks' plumage. The tail is again fanned, the wings drooped and spread to a considerable extent, the head held down and forward. In this attitude the cock passes first on one side of the hen, then on the other, and as he passes he tilts his body so that the brilliant upper surface of body and wings is towards the hen.

The hen may "reject" her suitor, by simply walking on to the station of the next male; the males have no means of enforcing their desires if she does not show her approval, which she signifies by stooping and finally crouching in the position for coition. A hen may be courted unsuccessfully by several cocks and then choose (*choose* is the only correct word) another; or she may leave the ground without favoring any of them. From Selous' observations (for the details I must refer the reader to the original) it is quite clear that the hens come to the ground for a definite purpose — to be stimulated sexually, to put it in the most physiological way — and if the stimulus is not sufficient they leave the ground without coition taking place. The stimulus is given by the display of the cocks, and one may be successful where another fails; success depends therefore on the variations in the males, or on the whim of the female, or, most probably, on both combined.

The fighting, finally, is very curious. There are a great many warlike preliminaries, a good deal of sparring and feinting, but only once in a long while any real hard fighting, such as many smaller birds indulge in— Tits and Thrushes, for instance. The whole business comes to be half ludicrous, half contemptible to watch. Selous' idea is that it has degenerated from real fighting and is now fixed as a ceremonial action. At any rate it appears never to decide anything— nor does it seem to have any influence whatever on the hens. In this species, then, we have a fine "expression of emotion" in the shape of the Dance, but here it is confined to one sex instead of existing in both, as in the Grebe. We have also a Display as a direct stimulus to coition, and working out in such a way as to make Darwinian Sexual Selection operative; and we have sham Fights, whose downward development has probably gone hand in hand with the upward development of the Display.

As a third, and again very different form of history, let us take that of the majority of the Old-world Warblers (*Sylviidæ*) so thoroughly worked out by Eliot Howard ('07). These birds include a number of famous European songsters, such as the Black-cap, Garden Warbler, and Marsh Warbler. They are mostly of very sober plumage, with little or no sexual dimorphism (though to this the Black-cap is an exception). The majority of the forms are migratory, and it is to these that we will confine our attention.

The course of events is similar in almost all the species. In March and April the birds come over to England from the South, in flocks and bands, which, following the river valleys, gradually split up as they spread over the country. The influx of migrants occurs in successive waves, and an important point to notice is that the arrival-period of any species takes a considerable time. The average immigration period lasts for about four weeks, but in some species it is only about three, while in others, like the Chiff-chaff it may extend to seven (and in some species of the closely related *Turdidæ*, even to 9 or 10 weeks).¹ Nests with eggs are usually found before the migration is complete.

¹ See Annual reports on the immigration of summer residents, published in Bulletins of the Brit. Ornithol. Club from 1906 onwards.

In all the species, the male arrives a week or more in advance of the females; this week is spent in the acquisition of a definite Territory, or sphere of influence; each cock probably returns to the place where he was hatched and reared, and this inevitably gives rise to disputes. From Mr. Howard's observations it is quite clear that this "Territorial System" is here, as in many other birds, of the greatest importance in the affairs of the species, and if trespassing takes place, violent conflicts ensue until one bird is in undisputed possession, which fact he proclaims by his song. Then the females arrive; they too presumably re-traverse the routes they followed southwards in the previous autumn, they hear the songs of their mates, and come down to the nesting-sites thus already staked out for them. It would appear that, while the cocks fight for the occupation of a territory, the hens fight too — for the right of entry into the territory once it has been gained by the cock. In these female combats the cock seems to take very little active interest, so that pairing-up is apparently scarcely influenced at all by individual likes or dislikes (a primitive condition, and very unlike what occurs in the Grebe) — there is simply an impulse to sing and so to attract mates in the male, in the female an impulse to pair-up with any male in possession of territory. It is only after this that "courtship" begins. Nest-building, coition, and courtship all start almost immediately after pairing-up. The courtship has the form of a display by the cock, who hops about in front of the female in the display-position found in so many birds, with head low and outstretched wings drooped and extended, tail fanned and raised; often too he holds a leaf or twig in his beak.

The female will often remain absolutely unmoved by these displays, feeding as unconcernedly as if the cock and his frantic ecstasy were a hundred miles away; but when coition takes place it seems to do so as a result of the hen being first in a receptive condition, and then being stimulated by this display of the cock.¹

¹ Critics of such a view as that here adopted to explain the habits of the Warbler, and adopted in general by Pycraft ('13), would do well to remember that in all the higher animals the *condition of the brain* very largely determines action. The cock is more eager than the hen. Her mere presence will inspire him with the desire to pair, but only at intervals; when this desire is present, he expresses it in the display actions. These actions in their turn inspire the hen with the desire to pair — but again not every time that they are exhibited.

Display and coition go on until all the eggs are laid, and incubation then begins. This is usually a duty of the hen bird, and the cock generally continues singing till the young are hatched. As far as the race is concerned, the cock's song is to attract a mate and then probably help stimulate her; but as far as the cock bird himself is concerned, song is simply an outlet, and a pleasurable one, for nervous energy; thus, provided certain internal physiological conditions are fulfilled, he will continue to sing in all moments of excitement or exaltation, non-sexual as well as sexual.¹ After hatching-time however, it is necessary that he help feed the young, and his nervous energy being thus diverted, his song ceases.

In these birds, it appears to me that we are being shown some of the primitive things of courtship. In this, Mr. Pycraft and myself are, I think, agreed; to both of us the "display" of the male Warbler is nothing but a *direct* expression of sexual excitement, scarcely, if at all, modified by Darwinian Sexual Selection — nothing but the way in which nervous disturbance caused by sexual excitement happens to liberate itself. General nervous discharge will cause general muscular contraction; and something approaching this is here seen — rapid hopping, extension and fluttering of the wings, spreading of the tail, bristling up of the feathers on head and throat, and the utterance of a series of quick sounds. This expresses a condition of readiness to pair, and doubtless to the female comes to be a symbol of the act of pairing. Hence, as far as the female is concerned, the act of pairing has come to depend upon this stimulus (acting of course on a suitable internal physiological state). This is no more strange in the bird than it is that in ourselves thoughts and emotions of love well up at the sight of some tangible object connected with the beloved. The main difference between the Grebe and the Warblers in this respect is that in the Grebe both sexes are equal in their affection and also in their eagerness, while in the Warblers the hen, as evidenced by her behavior, is most obviously less eager than the cock.

An extremely similar form of courtship, especially as far as the

¹ As is well known, many birds sing under the influence of anger (*e. g.* the Reed-warbler, *Acrocephalus streperus*), or as a result of a sense of general well-being (*e. g.* Song-thrushes, *Turdus musicus*), on warm days in winter.

relations of display and coition are concerned, is found in such birds as most Finches. These are monogamous, and the male only goes through a display. But here there is almost always sexual dimorphism, the cocks often being very brilliant, and the brilliant colors are so arranged that they are especially well shown during display. Here then some agency must have been at work, adding to the primitive display of the Warblers, and making it more effective as a stimulus to the hen.

These three different courtships give us, as I believe, the key to the general problem of courtship in birds. To me, that key consists in this: — that under the one term “Courtship” are included two entirely different sets of activities. In the first place, there are such activities as are shared equally by the two sexes — ceremonies and actions, often elaborate, performed for the pleasure and the joy of the performance; and secondly, there are ceremonies of the nature of a display by one sex only. I would prefer not to have to give special names to these two distinct sets of activities until I have more facts and more fully-digested facts; but to distinguish between them, I propose here to give the name of *Display Courtship* or *Darwinian Courtship* to the second set of activities; and to the first, which has scarcely received any of the attention it deserves, either from Darwin or subsequent authors, I shall give the name of *Mutual Courtship*.

As far as I can see, the underlying physiological bases for these two forms of courtship are to be found in the inherited sexual temperaments, if one may so call them, of the two sexes. In some birds, the male is much more eager than the female, and it is in these that Display Courtship has developed. The basis for Mutual Courtship lies in a similarity of sexual temperament in both sexes — neither markedly more eager nor more reserved than the other.

Furthermore, the immediate function of courtship is twofold. Either form of courtship may have both functions; it may serve, first, as a stimulus to coition (in Mutual Courtship the pair is worked up, in Display Courtship the male works the female up to the necessary point of exaltation); and secondly it may serve as a bond to keep the pair together.

In mutual courtships, the tendency is to drop the first function

(as in the Grebe); in Display Courtships, to drop the second (as in the Warblers). As a special development of the Display Courtships we get courtships like those of the Blackcock.

It is interesting to note the relation of Darwinian Sexual Selection to these various categories.

Darwinian Sexual Selection obviously does not operate in primitive display courtships like that of the Warblers, nor in Mutual Courtships. On the other hand, Selous' work shows that it does operate, with almost diagrammatic clearness, in the Blackcock. In the case of monogamous birds in which the males only have brilliant colors, I should like to reserve judgment. But there is another point; all courtship, it is here maintained (as also by E. Howard and by Pycraft) has had its origin in posturings and actions that are merely the direct outcome of sexual excitement, so that one finds birds without any special sexual structures or colors going through actions that are of the nature of courtship, be it mutual or be it Darwinian (take as example the Gulls on one side and the Sylviidæ on the other). Then it is clear that the development of special colors and structures employed in courtship must be a later addition, due to some separate influence, and this holds true both of structures (like the Grebe's crest) used in mutual courtship, or those (like the crest of the Ruby-crowned Kinglet) used in display courtship. These latter, as I say, may perhaps owe their origin to Darwinian Sexual Selection. The former cannot, so we must revise our theories in the light of this new conception of Mutual Courtship.

Mr. Selous has a very interesting chapter on this subject. (Selous, '05. "Inter-sexual Selection," pp. 261-283), to which, however, my attention has only just been drawn. My own conclusions, though similar in many ways, were reached entirely independently (Huxley, '14, pp. 523-525).

It is necessary to observe that in most birds, as in Man himself, the two forms of Courtship are inextricably interwoven. Man is one of the most complicated of all, for while much is absolutely reciprocal, yet there is much that is not mutual, and it is almost impossible not to believe that here at least there has been a double action of Darwinian Selection, the ancestral appearance of both man and woman having been modified in different ways through its agency.

The facts given above and their discussion will serve to make clear some of the general principles and problems of courtship in birds. Our next business is to get an insight into the interpretation of observations on birds. The connected descriptions I have given of the life-histories of various birds have only been made possible, first by the collection of a great many facts, and secondly by the interpretation of those facts; and the second is as important as the first.

It is indeed almost impossible to collect valuable facts unless one has some idea of how they are to be interpreted, and to those who are interested in this subject, I would say this: — remember the multifarious aspects from which any fact of bird-behavior can and should be looked at.

Take the case of any elaborate courtship action, such as the ‘shaking’ of the Grebe, or the dance of the Blackcock. There are two main points we want to understand; what is the meaning to-day? and what has been the origin in the past? And to answer these we have first to ask, and answer, the following questions: —

First, can we see any utility in it? if so, is it of use (a) simply to the species as a species, or is it of use (b) to the individual, (c) the pair, or (d) the family, and so indirectly to the species?

Secondly, can we see anything which is not of definite biological utility in the character? if so, what is the reason for the presence of this non-utilitarian factor? Is it (a) purely accidental? (b) determined through the inheritance of characters once useful, but now no longer so? (c) a matter of physiological correlation — that is to say, dependent on the general structure and working of the rest of the body? (d) dependent on the structure and working of the mind — a matter of psychological correlation?

Let us analyse the above examples in the light of these questions. The mutual head-shaking of the Grebe is apparently of use, like all the other mutual courtship actions, in keeping the pair together during the breeding season. It is then of direct biological use to the pair regarded as a unit of the race, and to the next generation. Besides this, it may be of some slight advantage to the individuals as liberating the energy of the sexual period in a harmless and pleasurable manner; but as far as origin is concerned, the survival value of the character — the handle by which Mutual Selection

can seize hold of it — is given entirely by its value to the pair and to the offspring.

On the other hand, many of the details of the ruff itself, and of the mode of shaking, are non-utilitarian. To carry out its function successfully, any courtship-action must stimulate the senses in a way which must be either pleasurable or startling, or a combination of both, and to this condition the erected ruff of the Grebe conforms — it affords a brilliant combination of black, chestnut and white, which, in addition, is only revealed when the ruff is erected. The general principles of the action are thus determined; but the origin of many of the details we can only look upon as accidental. As far as the position and color of the ornament is concerned we can only say that the Grebe family “shows a tendency” to develop crests and ruffs on the head, and that any brilliant pigmentation they possess runs to black, warm browns, yellows, and whites, while that of other birds runs to other colors — in the Woodpeckers to scarlet, in the Parrots largely to greens and yellows, and so forth. These things are “accidents,” in the sense that they are determined by unknown peculiarities in the constitution of the species.

The *form of the action* itself, however, is largely a matter of correlation. Many water-birds can be seen to shake their heads from side to side at intervals, especially after preening themselves, and from observations on the curious connection between this courtship-action and actual preening in the Grebe, I have no doubt that it is a specialization of the casual head-shaking after preening.¹

Finally there is a modification of the typical action of shaking which is seen under the influence of jealousy, and is characterized by exaggeration of all the normal behavior (Huxley, '14, p. 511). This is a matter of psychological correlation — take a Sensori-motor arc connected with mental processes; increase the intensity of the mental processes, and you increase the intensity of the actions which are the end, *i. e.* result of that activity.

To get an example of an action which is determined through inheritance alone, we must go to another species. The Ringed

¹ Huxley, '14, p. 515. In a similar way the elaborate courtship ceremonies, as seen in the Grebe and many other species, in which twigs are used and held in the bill, doubtless take their *origin* in nest-building.

Plover, for instance, (*Ægialitis hiaticula*) usually breeds on the seashore, and there lays its eggs among the stones. A certain number, however, breed on inland heaths, but even these pave their nests with small stones (Newton, '93, p. 482).

Such a discussion will make it easier to comprehend that it is possible to answer in various ways that question "why does such-and-such a species of bird perform such-and-such an action?" "Why do the Grebes shake their heads at each other?" The Evolutionist answers that the cause lies in Mutual Selection, which has developed the action for the good of the race. The Physiologist sees the reason in the activity of the gonads; these exert by chemical means a stimulus on the nervous system, which in its turn is arranged in such a way as to cause the stimulus to run down and set the appropriate muscles to working. The Psychologist sees in it a self-exhausting psychological process accompanied by a pleasurable expression of emotion — the bird does it because it enjoys doing it. In reality, all are right — in their degree; and it is from a failure to get a sufficiently broad point of view, a failure to distinguish between ultimate cause, immediate cause, and mere necessary machinery, that so much of the barren disputes of biology are due.

(*To be concluded.*)